

## 6.—Geographic races of the agamid lizard *Amphibolurus caudicinctus*

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Manuscript received 21 February 1967; accepted 21 March 1967

### Abstract

*Amphibolurus caudicinctus* (Günther) occupies rocky habitats in the western two-thirds of Australia, north of latitude 29°S. It breaks up into at least 7 subspecies: *caudicinctus* (syn. *imbricatus* Peters), *mensarum* nov., *injans* nov., *graafi* nov., *rufescens* Stirling & Zietz, *slateri* nov., and *macropus* nov. Other populations, not yet identified to subspecies, are mentioned. Some aspects of the species' ecology are discussed, including evidence that members of the nominate race live for little more than a year.

### Introduction

*Amphibolurus caudicinctus* is abundant in the rocky hills of the Pilbara-Hamersley region of Western Australia (which includes the type-locality). Elsewhere it is not so continuously distributed and is much less plentiful, at least in collections. It has therefore not been easy to characterise the numerous, more or less disjunct populations beyond the range of the nominate race, or to fix their geographic limits. This attempt to do so will doubtless require amendment as material from critical areas becomes available.

The races described herein are based almost entirely on adult male characters. In females and juveniles, geographic variation in colour pattern is largely obscured by individual variation and ontogenetic change. As a result, samples lacking fully adult males have generally not been determinable to subspecies.

In the following descriptions snout-vent length has been abbreviated to SVL. Numbers in brackets after ranges in quantitative characters are means. Measurements (summarised in Table 1) were made as in Storr (1965, p. 52). Upper labials were counted along the series of rectangular scales to the point where the outline of the lip begins to deflect downwards and backwards to the rictus; the irregularly shaped and sized scales posterior to this point were excluded.

The prefixes R, NTM, SAM and USNM refer to specimens respectively in the collections of the Western Australian Museum; Animal Industry Branch, Northern Territory Administration, Alice Springs; South Australian Museum, Adelaide; and Smithsonian Institution, Washington. For the loan of these external specimens I am indebted respectively to Mr. K. R. Slater, Mr. F. J. Mitchell and Dr. J. A. Peters. I am grateful to Mrs. A. Neumann (Librarian, Western Australian Museum) for translations of Peters' and Sternfeld's papers.

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### General description of *A. caudicinctus*

Limbs and tail long (see Table 1). Nuchal crest a series of small, contiguous, laterally compressed spines. No dorsal crest (though a slight mid-dorsal ridge may be formed by perfectly aligned keels of enlarged, slightly raised, vertebral scales). Nostril much nearer to orbit than tip of snout, located on or immediately below swollen rostral ridge (acute in *rufescens*), entering downwards and slightly forwards. Strong gular fold extending obliquely back on to side of neck. No dorsolateral fold (except possibly in *rufescens*).

Scales on top of head unicarinate, becoming small and subtubercular on occiput. Dorsal scales small to moderately large, increasing in size towards enlarged vertebral series, imbricate, mucronate or spinose, strongly or weakly unicarinate, alignment of keels converging back towards midline. Lateral scales much smaller, arranged in transverse whorls, weakly imbricate, smooth or weakly unicarinate, their keels (when present) directed backwards and downwards. Scales on upper surface of limbs similar to but larger than dorsals. Gular and ventral scales weakly imbricate, smooth or feebly keeled.

Upper labials 12-19. Subdigital lamellae bispinose, 21-35 under fourth toe. Femoral and preanal pores in both sexes and all ages, 23-62, each located between a slightly raised clump of 4-5 scales, extending nearly to end of thigh and interrupted at midline.

### Key to adult males

1. Nasal well below acute rostral ridge; pores more than 44 ..... *rufescens*  
Nasal on or just below swollen rostral ridge; pores fewer than 43 ..... 2
2. Whole of tail compressed; dark narrow caudal bands encircling tail ..... *caudicinctus*  
Base of tail not compressed; dark caudal bands (if any) not extending to lower surface ..... 3
3. Adpressed hind-leg not extending to end of snout ..... 4  
Adpressed hind-leg extending past snout ..... *macropus*
4. Keels of dorsal scales sharp and black ..... *slateri*  
Keels of dorsal scales obtuse and not black ..... 5
5. Back reddish; hind-leg and base of tail obscurely banded with dark brown ..... 6  
Back yellowish; hind-leg and base of tail not banded ..... *graafi*
6. Paravertebral spots obsolescent ..... *mensarum*  
Paravertebral spots persistent ..... *injans*

TABLE 1

Mean length of head, tail, foreleg and hindleg, expressed as per cent. length of trunk; and mean width of head, depth of head and diameter of ear-aperture, expressed as per cent. length of head (all with standard deviations in brackets).

	Sample Size	Per cent. Length of Trunk				Per cent. Length of Head		
		Head	Tail	Foreleg	Hindleg	Head Width†	Head Depth	Ear
<i>caudicinctus</i>	37 ♂	41.5 (2.2)	321 (17)	62.2 (3.7)	127.2 (7.3)	78.5 (3.7)	59.0 (5.1)	15.8 (1.8)
	35 ♀	36.8 (2.1)	284 (15)	58.2 (3.4)	118.9 (7.8)	76.7 (3.1)	56.0 (3.7)	17.7 (1.6)
<i>mensarum</i>	8 ♂	41.1 (1.1)	312 (10)	59.4 (3.1)	126.6 (4.7)	79.9 (4.3)	57.0 (1.9)	17.2 (1.8)
	1 ♀	37.8	291	56.7	126.3	83.5	54.1	17.7
<i>infans</i> ....	2 ♂	37.0	277	54.0	115.5	84.0	56.0	15.5
	2 ♀	37.0	244	52.2	110.5	82.8	55.0	15.0
<i>macropus</i>	2 ♂	37.8	354	61.6	139.0	79.8	60.9	19.4
<i>slateri</i> (1) ... ..	10 ♂	37.8 (1.8)	306 (11)	60.5 (2.5)	122.9 (3.5)	78.0 (2.9)	54.7 (3.0)	17.2 (1.8)
	12 ♀	34.5 (2.1)	272 (16)	55.2 (2.9)	114.0 (4.8)	79.5 (2.9)	57.2 (3.6)	19.2 (1.7)
<i>slateri</i> (2) ... ..	8 ♂	38.0 (1.8)	317 (6)	59.3 (2.2)	120.7 (5.5)	75.9 (3.0)	55.8 (3.5)	16.8 (1.7)
	3 ♀	35.0 (2.4)	283 (8)	56.7 (3.1)	112.3 (6.4)	80.3 (4.5)	56.8 (3.9)	17.3 (1.7)
<i>graufti</i> ....	20 ♂	41.4 (2.1)	335 (21)	62.6 (2.9)	129.0 (4.8)	79.0 (4.2)	57.4 (3.8)	17.4 (1.6)
	11 ♀	39.2 (2.0)	303 (11)	60.1 (2.0)	120.4 (5.7)	76.1 (3.0)	54.4 (2.2)	18.2 (1.6)
<i>rufescens</i> ... ..	6*	38.2	316	61.1	127.8	75.3	49.3	16.7

\* Entire Series.

† Includes jowls, which masks the relative narrowing of skull in maturing males of *A. c. caudicinctus*.

(1) Hermannsburg Series.

(2) George Gill Range Series.

### *Amphibolurus caudicinctus caudicinctus* (Günther)

*Grammatophora caudicincta* Günther, 1875, in Richardson & Gray's "Zoology of the Erebus and Terror" 2: 19. Nickol Bay, Western Australia (F. H. du Boulay).

*Amphibolurus imbricatus* Peters, 1877, Mber. Preuss. Akad. Wiss. 1876: 529. Mermaid Strait, Western Australia (SMS "Gazelle").

**Distribution.**—Pilbara region of Western Australia from the De Grey River south to the Hamersley, Ophthalmia and Robertson Ranges. Also on Depuch Island, Dolphin Island (Dampier Archipelago), Monte Bello Islands (*vide* Hill 1955), and Barrow Island.

**Description.**—Juveniles dorsally reddish brown, dotted with black or dark brown. Two longitudinal series of dark spots arranged in pairs, one on each side of midline. Usually greyish white lines across body and tail alternating with dark paravertebral spots. Underneath whitish except for throat which may be flecked or dappled with grey.

As females mature, transverse whitish lines disappear from back, and dark spaces between pale caudal rings contract to form brown bars. Paravertebral spots become paler and usually disappear.

As males mature, tail and (to smaller extent) body become laterally compressed, head narrows and deepens, fleshy jowls develop about posterior corner of jaw, and throat swells. Head and back dull blood-red, colouring on flanks tending to concentrate in three wavy longitudinal streaks. Rump and upper surface of limbs olive grey. Tail yellowish brown (darker proximally), completely or almost completely encircled by blackish brown bands much narrower than pale

interspaces. Underneath whitish except for black patch on chest and grey marblings on throat.

Upper labials 12-19 (15.4). Lamellae under fourth toe 21-32 (27.2). Femoral and preanal pores 23-40 (31.5). Maximum SVL: Males 89, females 74.

**Remarks.**—In coloration and habitus adult males of this race diverge from juveniles and females to a much greater extent than in other races. Consequently workers with scanty material have understandably failed to identify *imbricatus* (based on juvenile) with *caudicinctus* (based on adult male), even though their type-localities are only 20 miles apart.

Another thing that has delayed the laying of the *imbricatus* ghost is that workers have referred to Boulenger's (1885: 382) description of a South Australian "*imbricatus*" rather than to the original description. The notion thus arose that *imbricatus* was the eastern representative of *caudicinctus*. In other quarters "*imbricatus*" has been applied to juveniles generally.

**Material.**—Western Australia; North-West Division: R 2121 (De Grey); R 9867 (Strelley); R 19423 (Roebourne); R 17021, 17052-3 (Nickol Bay); R 19424-6 (Karratha); R 19378-82, 19427-8 (Erramurra Creek); R 13874 (Andover); R 13875 (Lilley B. Mine, via Roebourne); R 19432-42, 20205, 20207-11, 20218, 20221, 20225 (Mt. Herbert); R 19430-1 (Daniels Well); R 19443-57, 20228-9 (Millstream); R 20213, 20233 (Kangiangi); R 20227, 20231 (Mt. Ulric); R 19458-61 (21 mi. W of Tambrey); R 20216, 20220 (Pindrina Waters, 20 mi. NW of Tambrey); R 20212, 20219, 20224 (Tambrey); R 20206, 20214-5 (Tanberry Creek); R 10810 (Hooley);

R 19463 (16 mi. NW of Wittenoom); R 20217, 20222-3, 20226, 20230, 20232 (Asbestos Creek); R 13997 (Wittenoom); R 19465-6 (Yampire Gorge); R 13138, 19467-79 (Dales Gorge); R 13315, 13424, 19422 (Woodstock); R 10797-800 (Abydos); R 19410-21 (Marble Bar); R 11339 (Limestone); R 19388-409 (Mt. Edgar); R 19386-7 (Meentheena); R 14586-7 (Braeside); R 13254, 13259 (Mosquito Creek); R 13168 (Nullagine); R 19481 (14 mi. N of Roy Hill); R 19480 (17 mi. E of Marillana); R 17688, 25133-4 (Turee Creek); R 23985-6 (Mt. Newman); R 24012-4 (25 mi. NW of Mundiwindi); R 13338-9, 13603, 25210 (Jigalong). Eastern Division: R 25180-3 (20 mi. E of Jigalong). Islands off North-West Coast: R 14548-9, 14551, 14554, 14560-2 (Depuch); R 14252, 14280-3, 14293-5, 14299, 14328 (Dolphin); R 12890-1, 12893 (Barrow).

***Amphibolurus caudicinctus mensarum***  
subsp. nov.

*Holotype*.—R 19486 in Western Australian Museum, an adult male collected by G. M. Storr on February 2, 1961, 5 miles south of Meekatharra, Western Australia, in 26° 40'S, 118° 27'E.

*Distribution*.—Murchison and East Murchison Goldfields of Western Australia from Mileura east to Mt. Fisher.

*Description*.—Head of adult male not so narrow or pointed as in nominate race and jowls less developed. Throat not swollen. Body depressed. Only distal part of tail compressed. Dorsal coloration duller, i.e. pale reddish brown. Caudal bands paler (i.e. brown) and not extending to lower surface. Hind-legs reddish brown, banded with olive or dark brown.

Females and juveniles differ from those of nominate race mainly in having larger, darker and more numerous dorsal spots (paravertebral series narrowly separated, adjacent spots occasionally coalescing to form short transverse bars).

Upper labials 12-17 (15.5). Lamellae under fourth toe 21-30 (25.2). Femoral and preanal pores 28-37 (33.6). Maximum SVL: males 81; females 62.

*Remarks*.—As discussed later under populations *incertae sedis*, this race intergrades with typical *caudicinctus*. If a boundary can be defined between them, it will probably be found to lie along the Ashburton River and Ilgarri Creek.

*Paratypes*.—Western Australia; North-West Division: R 15754, 15771-2, 15790-4 (Mileura); R 19482-5 (14 mi. N of Meekatharra). Eastern Division: R 21115-8 (Wiluna); R 13700 (Mt. Fisher, 110 mi. E of Wiluna).

***Amphibolurus caudicinctus infans***  
subsp. nov.

*Holotype*.—R 25945 in Western Australian Museum, an adult male collected by G. M. Storr and W. H. Butler on November 7, 1965, at Deeba Rock-hole, 25 miles north-east of Laverton, Western Australia, in 28°22'S, 122°35'E.

*Distribution*.—Mt. Margaret Goldfield of Western Australia from Laverton south-west to Kookynie.

*Description*.—Considerably smaller than *mensarum*, with appendages relatively shorter and adult coloration scarcely different from juvenile.

*Adult male*: Head relatively short and broad; no jowls. Body slightly depressed. Tail not compressed. Dorsally reddish brown (with paler and duller vertebral streak); dotted with black, especially on head. Blackish longitudinally elongate paravertebral spots alternating with transverse rows of small pale pinkish brown or pinkish white spots. Lateral and dorsolateral surface with black and dark brown variegations including a dorsolateral series of crescentic spots. Ventrolateral surface of abdomen suffused with mustard-yellow. Hind-leg and base of tail obscurely and narrowly banded with greyish black. Remainder of tail broadly barred with dark greyish brown, 3-4 times as wide as pale interspaces. Lower lips vertically barred with dark grey. Throat dappled with grey. Black pectoral patch long and narrow, extending acutely on to abdomen, whence it continues as a grey streak to vent. Lower surface of distal segments of limbs dark grey. *Juvenile and adult female*: Body strongly depressed. Dorsally brick-red or orange brown, dotted with black or dark brown. Small, elongate, dark-brown paravertebral spots, forming on tail a single series. Pale transverse lines well developed on back and tail. Vertebral streak pale. Lips vertically barred with pale grey. Throat variegated with grey.

Nuchal crest very weak. Vertebrae scarcely differentiated from other dorsal scales. Dorsal keels strong, mucronate to subspinose. Upper labials 13-17 (14.3). Lamellae under fourth toe 22-25 (24.0). Femoral and preanal pores 32-42 (37.3). Maximum SVL: males 67, females 59.5.

*Paratypes*.—Western Australia; Eastern Division: R 25946-8 (25 mi. NE of Laverton); R 22583-4 (Mt. Morgans); R 15725, 22588-9, 25911 (Niagara Dam, 7 mi. SW of Kookynie).

***Amphibolurus caudicinctus graafi*** subsp. nov.

*Holotype*.—R 25914 in Western Australian Museum, an adult male collected by G. M. Storr and W. H. Butler on November 4, 1965, at Mt. Eveline, Western Australia, in 26°10'S, 127°06'E.

*Distribution*.—Hills and granite outcrops of far eastern interior of Western Australia, from Warburton Range east to Barrow Range.

*Description*.—*Adult male*: Body depressed. Base of tail subcircular in section, slightly flattened on top. Dorsally dull yellowish brown (reddish in preservative). Dark paravertebral spots persistent only in smallest specimens. Legs and base of tail unbanded. Distal three-quarters of tail obscurely barred with dark greyish brown, more than twice as wide as pale interspaces. Flanks and dorsolateral surface of body dark grey (except for indistinct pale dorsolateral stripe in some specimens). Black pectoral patch larger than in other races (except *macropus*), narrowly extending on to anterior part of abdomen and often on to lower surface of arm. Throat with or without pale grey

variegation or obscure reticulum. Vicinity of gular fold suffused with salmon pink. *Adult female*: Dorsally reddish brown (brighter than male), flecked with blackish brown. Two rows of blackish brown paravertebral spots not widely separated and not well-aligned transversely. Occasionally a dorsolateral series of smaller spots. Scarcely any trace of transverse rows of pale dots.

Nasal on swollen rostral ridge. Keels of dorsal scales obtuse, weak to moderately strong, mucronate, concolorous with rest of scale. Ventrals smooth, sometimes feebly keeled on chest of males. Upper labials 14-20 (16.4). Lamellae under fourth toe 25-30 (27.2). Femoral and preanal pores 29-39 (34.6). Maximum SVL: males 79, females 72.

*Remarks*.—This race is named after Mr. Mark de Graaf, an Honorary Associate of this Museum, who collected many reptiles during his term as headmaster of the Warburton Range school. The local aboriginal name for this lizard is "tantalka" (M. de Graaf).

*Paratypes*.—Western Australia; Eastern Division: R 21999 (Granite Spring, 18 mi. NE of Warburton Range Mission); R 22037, 22195-6 (Windarro Spring, 1 mi. E of Granite Spring); R 19488, 25915-38 (Mt. Eveline, 38 mi. E of Warburton Range); R 15716-7 (13 mi. NE of Mt. Eveline).

***Amphibolurus caudicinctus rufescens***  
Stirling and Zietz

*Amphibolurus rufescens* Stirling & Zietz, 1893, Trans. Roy. Soc. S. Aust. 16: 164. Mt. Sir Thomas, Birksgate Range, South Australia (Elder Expedition).

*Distribution*.—Far north-west of South Australia, south to the Birksgate Range and east to Granite Downs.

*Description*.—Head and body depressed. Tail proximally circular in section or flattened on top, slightly compressed distally. Nasal below relatively acute rostral ridge in adults; on swollen rostral ridge in single juvenile. Nuchal crest very weak in juvenile, stronger in adults. Dorsals small, keels weak and obtuse. Keels of laterodorsals reduced to small tubercles. Vertebral scales scarcely distinguishable from adjacent dorsals and thus not forming vertebral ridge. Spines above, behind and below ear strongly developed. Gulars weakly tuberculate and ventrals weakly keeled in juvenile; smooth in adults.

Upper labials 15-17 (15.3). Lamellae under fourth toe 26-33 (29.0), spines not dark. Femoral and preanal pores 32-62 (mean 53.2, but only the juvenile has less than 45). Maximum SVL 92, but Zietz (1915) measured 97mm in a specimen from Wantapella (5 mi. SW of Granite Downs HS.).

Dorsally "rusty-brown" (Stirling & Zietz). Series of dark spots on each side of midline, narrowly separate; spots may be circular, longitudinally elongate, or coalescing into wavy stripe of irregular width. Dark dorsolateral markings (dashes or crescents) orientated longitudinally and tending to coalesce. Vertebral and dorsolateral spots transversely elongate

on base of tail and tending to coalesce into narrow, widely separate, ill-defined bars. Distal half of tail faintly barred with dark brown. Upper surface of limbs obscurely and irregularly barred with brownish black blotches. Throat marbled with dark grey. Male pectoral patch "olive", extending narrowly on to abdomen and sometimes on to anteroventral surface of arm.

*Remarks*.—It is with some diffidence that I treat *rufescens* as a race of *caudicinctus*; for the scanty material is old or poorly preserved and, coming from widely separate localities, is highly variable. My main reasons for doing so are that *rufescens* is clearly a representative of *caudicinctus* and differs from other representatives in only two important respects; the numerous pores and the nostril located well below the sharp rostral ridge; but even these "key characters" are lacking in the single juvenile (SAM 1425).

With its weak nuchal crest and dorsal keels and in the colour pattern of the flanks, base of tail and upper surface of legs, *rufescens* shows some resemblance to *infans* from the other side of the Great Victoria Desert. The tendency for dorsal keels to be black points to the Central Australian populations. But apart from its long appendages, *rufescens* shows little resemblance to its nearest neighbour, *graafi*. The systematic status of *rufescens* will thus remain in some doubt until the Cavenagh, Blackstone and Tomkinson Ranges are worked.

*Material*.—South Australia: SAM 1423 (holotype) and 1424-5 (paratypes) (Mt. Sir Thomas); SAM 5632 (Mann Range); SAM 586 (2 specimens, Everard Range).

***Amphibolurus caudicinctus slateri* subsp. nov.**

*Holotype*.—R 26793 in the Western Australian Museum (formerly NTM 1471), an adult male collected by K. R. Slater on February 11, 1964, at Hermannsburg, Northern Territory, in 23° 58' S, 132° 46' E.

*Distribution*.—Southern highlands of the Northern Territory from the eastern Macdonnell Ranges south-west to the George Gill Range.

*Description*.—*Adult male*: Dorsally dull fawn, vaguely and narrowly banded with pale brown on distal (and occasionally proximal) part of tail. Small dark paravertebral spots occasionally persistent. Head and flanks obscurely variegated with dark grey and often dotted sparsely with brownish white. Throat usually dappled with grey. Subtriangular patch on chest bluish or blackish grey. Slight rosy flush occasionally discernible behind pectoral patch.

*Adult female*: Dorsally pale, dull reddish brown (somewhat paler and brighter than in male), finely dotted with black. Paravertebral spots small, dark brown, the two series widely separate. Whitish dots may be present on back (especially dorsolaterally), usually without definite arrangement, occasionally in transverse rows. Throat dappled with dark grey.

Body depressed. Tail not compressed. Nasal immediately below obtuse rostral ridge. Keels of dorsal scales black, strong, sharp, terminating in spine. Ventrals smooth. Upper labials

12-17 (14.6). Lamellae under fourth toe 24-32 (28.0). Femoral and preanal pores 27-39 (32.0). Maximum SVL: males 83, females 69.

*Geographic variation.*—Coloration of the adult male, as given above, is based on topotypical material. In the George Gill Range, males differ in having (1) dorsum somewhat reddish on occiput, nape, arms and anterior part of back, (2) flanks obscurely variegated with dark brown, and (3) lower surface of arm and immediately behind gular fold orange-yellow. Specimens from George Gill Range also differ in their longer head and tail (see Table 1) and more numerous subdigital lamellae (averaging 28.6 under fourth toe, against 27.5 at Hermannsburg).

*Remarks.*—With its reduced sexual dimorphism, plain coloration and short appendages, *slateri* is very different from nominate *caudicinctus*. It is not surprising, then, that workers have had difficulty in placing Central Australian members of the species.

Specimens collected by the Horn Expedition at Alice Springs, Finke Gorge and Charlotte Waters were referred by Lucas & Frost (1896 : 126) to *A. imbricatus*. They pointed out discrepancies in coloration and number of pores between their specimens and Peters' original description.

Sternfeld (1924) had five specimens from Hermannsburg which he tentatively placed with *caudicinctus*. He was aware of their difference from typical *caudicinctus* in caudal coloration and length of limbs. Sternfeld drew attention to errors in Boulenger's (1885 : 384) description of *caudicinctus* and correctly prophesied that the species would prove divisible into several races.

Loveridge (1934 : 319) had a single specimen from Hermannsburg and, following Sternfeld, referred it (with specimens of *mensarum*) to *caudicinctus*, even though they keyed out to *imbricatus*. He suggested that *imbricatus* and *rufescens* were races of *caudicinctus*.

This race is named after Mr. K. R. Slater, in appreciation of the many courtesies he extended to the Western Australian Museum during his sojourn at Alice Springs. Mr. Slater kindly donated the holotype to this Museum.

*Paratypes.*—Northern Territory: SAM 3581 (between Alice Springs and Hart Range); R 20902 (Alice Springs); R 20869, NTM 1472-5, NTM 2379-96 (Hermannsburg); NTM 2378 (Palm Valley); NTM 2018-9 (Kathleen Creek, George Gill Range); NTM 1943, NTM 2670-9 (Reedy Creek, 6 mi. W of Kathleen Creek).

#### *Amphibolurus caudicinctus macropus*

subsp. nov.

*Holotype.*—R 3229 in the South Australian Museum, an adult male collected by R. R. Miller (American-Australian Arnhem Land Expedition) on September 30, 1948, 4½ miles south-southeast of Oenpelli, Northern Territory, in 12°23'S, 133°05'E.

*Distribution.*—North-western edge of Arnhem Land plateau, Northern Territory.

*Description (of adult male).*—Dorsally dull reddish brown with or without two widely separate series of small dark-brown paravertebral spots. Tail yellowish brown, banded on top and sides with dark brown; proximal bands ill defined, narrower than pale interspaces; distal bands darker and better defined. Black pectoral patch covering entire width of chest, beginning on gular fold and extending squarely back on to anterior part of abdomen (and in one specimen on fore-arm).

Much larger than other races (except *rufescens*), with relatively longer tail and hind-leg (see Table 1). Distal three-quarters of tail compressed. Nasal small, located on top of obtuse rostral ridge. Keels of dorsal scales moderately strong and sharp, terminating in mucron or short spine. Ventrals weakly keeled. Upper labials 15-16. Lamellae under fourth toe 31-35. Femoral and preanal pores 29-31. SVL: holotype 89, paratype 101.

*Remarks.*—In its great size, large pectoral patch, weakly spinose dorsal scales and compressed distal part of tail, *macropus* unexpectedly resembles *rufescens* from a thousand miles to the south.

*Paratype.*—USNM 128751 (same data as holotype).

#### *Incertae sedis*

Several collections made in winter contain only juveniles and subadults. While they are not identifiable to subspecies, these series help to fill out the range of the species and are listed below together with any data that indicate their systematic affinities.

1. *Ashburton, upper Gascoyne and Ilgararri Creek drainages (W.A.):* R 13923 (2 specimens from 10 mi. N of Mt. Wall); R 15819 (21 mi. NNW of Ullawarra); R 19429 (Barlee Range); R 22823 (18 mi. NW of Mt. Vernon HS.); R 25240 (foot of Mt. Vernon); R 22697 ("Mulgul or Mt. Vernen"); R 23997 (Kumarina); R 23933-4 (20 mi. NW of Beyonde); R 15843-4 (Weld Spring, Canning Stock Route); R 15839 (17 mi. N of Weld Spring).

The largest of these specimens, R 22697, is a male with SVL 74 mm. The base of its tail is slightly compressed, the legs are banded, and it retains paravertebral spots. It is thus an intergrade between *caudicinctus* and *mensarum*, but nearer to the latter. In contrast, a much younger male (SVL 61) from Turee Creek (50-80 miles further north and across the Ashburton) is indistinguishable from typical *caudicinctus*. In the larger (SVL 49.5) of two juveniles from near Mt. Wall (likewise north of the Ashburton) the tail is already beginning to compress; it is therefore likely that this population belongs to the nominate race, which is also to be expected on geographic grounds (Mt. Wall being a south-western outlier of the Hamersley Ranges). The young males from Beyonde resemble *mensarum* more than *caudicinctus*. The three juveniles from the Canning Stock Route are very reddish, like juveniles of *mensarum* from Wiluna.

- CAUDICINCTUS
- ▲ MENSARUM
- INFANS
- X GRAAFI
- RUFESCENS
- ▼ SLATERI
- MACROPUS

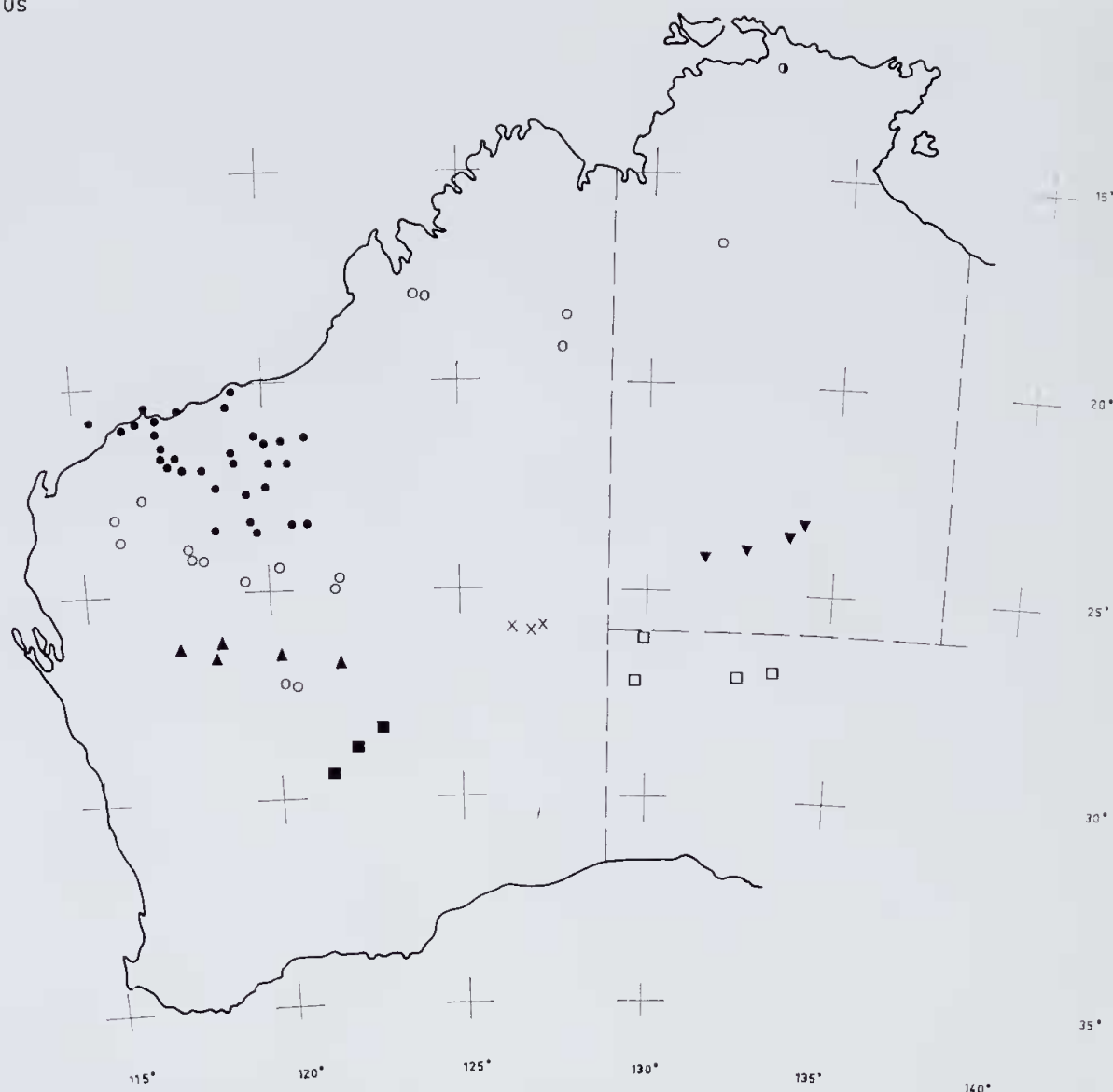


Figure 1.—Map of Western Australia, Northern Territory and north-western South Australia, showing location of specimens of subspecies of *Amphibolurus caudicinctus*. Specimens unidentified to subspecies are located by hollow circles.

2. *Barr Smith Range* (W.A.): R 19783 (Albion Downs); R 19487 (19 mi. NE of Kathleen Valley). The latter has an egg in the ovary. Though as large as a gravid *mensarum*, this specimen has a much shorter head and tail, in which respect it agrees with female *infans*.

3. *Victoria River drainage* (N.T.): R 13721 (Top Springs). This young male (SVL 61) is surprisingly similar to *slateri*, even to the strong black keels of the dorsal scales. Relative length of appendages is just within the upper limits of *slateri*. Its ventral scales are weakly keeled, a feature shared with *macropus* from 300 miles further north.

4. *Southern interior of Kimberley Division* (W.A.): R 26794 (Mt. Anderson); R 23032 (Grant Range, 3 mi. NW of Liveringa); R 23056-7 (20 mi. SE of Halls Creek); SAM 3573 (3 specimens from Wolf Creek).

Only R 26794 is fully adult—a female (SVL 72) collected in late May. It has a longer tail (316% of trunk) than any female of nominate race and a larger ear-aperture (20% of head-length) than all females of nominate race with

SVL greater than 63. Its dorsal coloration is dull reddish brown; the paravertebral spots are well developed anteriorly, but on posterior half of back they break up into transverse rows of small spots; also posteriorly the transverse rows of whitish spots persist.

The remaining specimens were collected in September, the largest (SVL 62.5) being a young male with blackish-grey pectoral patch. Their upper surface is uniformly pale brown, dotted finely with black; the paravertebral spots are small. In coloration they are thus similar to *slateri*, but disagree in their relatively long appendages and weak keeling of dorsal scales. The last feature also separates them from the specimen from Top Springs (300 mi. ENE of Halls Creek).

#### Ecology

#### Habitat

*A. c. caudicinctus* is widespread and abundant in the Pilbara, a region in which precipitous hills, razor-backed ridges of dolerite and piles of granite and other crystalline rocks are sel-

dom out of view. In most of this country *caudicinctus* is not only the commonest agamid, but few others are encountered apart from *Physignathus longirostris* which is largely restricted to wooded watercourses. It is only on the coastal plains and in some of the broader river valleys that *caudicinctus* becomes scarce or absent and other agamids (especially *Amphibolurus inermis* and *A. isolepis*) are plentiful. *A. c. caudicinctus* is not confined to rocky areas but may be found on plains of spinifex (*Triodia*) in the valley of the Fortescue, though generally only on heavy, stony soils shunned by *inermis* and *isolepis*. Here it occurs with *Amphibolurus reticulatus*, which however is scarce in this (the northernmost) part of its range.

South and south-east of the Ashburton River mountain ranges are fewer and widely separated. Here the undulating Precambrian Shield is not greatly dissected, and relief is provided mainly by buttes, mesas and "breakaways" (i.e. low cliffs leading up to minor plateaux). The vegetation is mulga scrub, which is notably deficient in ground cover. Suitable conditions for *A. c. mensarum* and *infans* are thus generally not plentiful or continuous, and moreover they must compete with increasing numbers of other agamids. *A. reticulatus* is common in stony areas, and *A. scutulatus*, *cristatus* and *ornatus* find their northern limits within the range of *mensarum*.

No form of *caudicinctus* has been collected in the eastern deserts of Western Australia, even though belts of residual sandstone commonly rise above the extensive areas of sand dunes. On the northern edge of the Great Victoria Desert, *A. c. graafi* shares with *Tympanocryptis lineata centralis* rocky habitats in the Warburton and Townsend Ranges. Further east it is replaced by *A. c. rufescens* which evidently occupies all the granitic hills of far northern South Australia. The several mountain ranges of Central Australia are usually separated by sandy lowlands unsuitable for the species. The resultant archipelagic kind of distribution lends itself to subspeciation, the full extent of which will not be appreciated until all these mountains are explored.

The highlands of the Kimberley Division, the watershed between the Victoria and Daly Rivers and the sandstone plateaux of Arnhem Land and the McArthur River are virtually *terra incognita* as far as their reptiles are concerned. They could well harbour abundant and diverse populations of *Amphibolurus caudicinctus*.

#### Breeding Season and Longevity

The precise date of collection is known for 165 individuals of our large series of *A. c. caudicinctus*. These break down by month, age and sex as follows. Range in snout-vent length is given in brackets.

**February:** 3 adult males (76-84); 7 adult females (62-70), all gravid except one (the largest).

**March:** 13 adult males (68-86); 23 adult females (57-72), all but five gravid; subadult male (65); 3 juveniles (25-48).

**April:** 4 adult males (77-83); 1 adult non-gravid female (74); 1 juvenile (25).

**May:** 2 adult males (81-89); 2 adult non-gravid females (61-63); 12 juveniles (23-46).

**June:** 1 adult male (80); 1 adult non-gravid female (70); 13 juveniles (28-50).

**July:** 2 subadult males (60-73); 17 juveniles (31-52).

**August:** 13 subadult males (56-68); 31 juveniles and subadult females (37-58).

**September:** 1 juvenile (56).

**October:** 1 adult male (75); 3 adult non-gravid females (59-69); 1 subadult male (62); 1 juvenile (55).

**November:** 3 adult males (71-80); 1 gravid female (67).

**December:** 2 adult males (75-76); 1 adult female (60); 1 juvenile (54).

Because the breeding season lasts for at least five months, it is not so easy to analyse the above data as was done elsewhere for the *Amphibolurus maculatus* species-group (Storr 1965). Nevertheless it seems fairly certain that *A. c. caudicinctus* breeds at about nine months of age and dies a few months later.

The eggs evidently hatch between January and May. Males begin to acquire adult characteristics (at SVL about 55) between June and September, mature between October and March, breed and continue to grow till the last of them die in early June. Females are gravid between November and March, continue to grow after laying, the last of them disappearing in early June.

#### Ecological effects on morphology

The races of *A. caudicinctus* can be compared with respect to relative length of appendages in Table 1 and better still in Table 2, which gives percentage departures from normal. "Normal" was obtained by averaging for each appendage the mean relative length in adult males of each race. Also given in Table 2 are mean latitude and mean annual temperature.

It will be seen that Allen's Rule (that appendages are relatively longer in warmer areas) is only partly followed here. Agreement is perfect in the series *caudicinctus*—*mensarum*—*infans*; but these are the only races that are contiguous and intergrading. Among the isolated eastern races there are numerous anomalies: the short head of *macropus*, the long head and tail of *graafi*, the short head and tail of topotypical *slateri* (compared to those of George Gill Range lizards), and the long appendages of *rufescens*.

Elsewhere it was established for the *Amphibolurus maculatus* and *reticulatus* species-groups (Storr 1965, 1966) that with decreasing temperature the number of upper labials increases and the number of subdigital lamellae decreases. Table 2 shows that the first of these generalisations does not hold here; on the contrary, labial counts are generally higher in warmer regions. The second generalisation does hold in the present species. In the western sequence, *caudicinctus*—*mensarum*—*infans*, lamellar counts steadily decline. In the eastern races counts are generally higher, but in *graafi* and topotypical *slateri* they are anomalously low.

TABLE 2

Mean latitude ( $^{\circ}$ S), mean annual temperature ( $^{\circ}$ F) and deviation (%) from normal in mean relative length of appendages of adult males and in mean number of upper labials and lamellae under fourth toe.

	Latitude	Annual Temperature	Relative Length of				Number of	
			Head	Tail	Foreleg	Hindleg	Labials	Lamellae
Western—								
<i>caudicinctus</i> ... ..	21.9	77	+ 6	+ 1	+ 3	+ 1	+ 1	- 2
<i>mensarum</i> ... ..	26.4	72	+ 5	- 2	- 1	0	+ 2	- 9
<i>infans</i> ... ..	28.9	68	- 6	- 13	- 10	- 8	- 6	- 13
Eastern—								
<i>macropus</i> ... ..	12.4	82	- 4	+ 12	+ 2	+ 10	+ 2	+ 20
<i>slateri</i> (1) ... ..	24.0	70	- 4	- 4	+ 1	- 2	- 4	- 1
<i>slateri</i> (2) ... ..	24.3	69	- 1	0	- 1	- 4	- 3	+ 3
<i>graffi</i> ... ..	26.6	71	+ 6	+ 6	+ 4	+ 2	+ 8	- 2
<i>rufescens</i> ... ..	26.8	69	- 3	0	+ 2	+ 1	0	+ 5

- (1) Hermannsburg Series.  
 (2) George Gill Range Series.

In the extreme depression of its head and body, *rufescens* approaches the south-western species *Amphibolurus ornatus*. It could well be that *rufescens*, like *ornatus*, is adapted for sheltering under slabs of exfoliated granite. At any rate it is closely associated with granitic rocks (White 1915).

At the opposite extreme to *rufescens* is adult male *caudicinctus*, whose compressed head, body and tail immediately separate it from all other races and cause it alone to resemble the arboreal agamids in habitus. Now adult males of the nominate race are commonly observed in the tops of shrubs and low trees, especially dead ones or on dead sticks. Almost certainly they are basking rather than feeding or taking refuge from predators. They quickly drop to the ground and seek terrestrial cover on the distant approach of an intruder, whereas the truly arboreal *Physignathus longirostris* is more likely to freeze or climb higher in the presence of man. No females or juveniles of *A. c. caudicinctus* have been observed in vegetation, nor any individual of other races.

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